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Research Article

Extinction risk alert: evaluating conservation trends for the Golden-dimpled Ground Beetle (*Carabus clatratus auraniensis* J. Müller, 1903) in Western Balkans

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Abstract

Due to extensive habitat loss and specialised ecological niche, the Golden-dimpled Ground Beetle (*Carabus clatratus*) became a locally extinct species with fragmented distribution throughout Europe. The subspecies *C. clatratus auraniensis* J. Müller, 1903 was described from the Vrana Lake in the Mediterranean biogeographical region of Croatia. This study aims to: assess conservation status of *C. clatratus auraniensis* in the Western Balkans through a chronogeonemy analysis; evaluate habitat suitability at the type locality by analyzing historical land use changes; and determine the effectiveness of protected area networks in ensuring the long-term survival of the species in core area of its distribution in Western Balkans. The chronogeonemy analysis reveals the extinction of *C. clatratus auraniensis* in the Mediterranean biogeographical region, including in its type locality. This is most likely caused by land use changes such as ongoing habitat degradation and wetland drainage, primarily driven by urbanisation and agriculture. However, the gap analysis indicated a good coverage by protected areas, contradicting previous results. The protected areas were established after the subspecies extinction and therefore have no impact on its conservation success. This indicates that gap analysis must be combined with other methods, e.g. chronogeonemy analysis, in order to detect real-time conservation trends. The conservation status of *C. clatratus auraniensis* in the Continental biogeographical region is stable, with continuous occurrence since the late 19th century and an increase in records in the last three decades, even with long dispersal records (e.g. Mura River in NE Slovenia). Records increase are linked to large well-preserved semi-natural wetlands along the Sava, Drava and Danube rivers, reflecting the subspecies' good prospects. Reintroduction into protected areas in the Mediterranean region of Croatia could be a viable strategy to support the survival of this subspecies, enhancing the conservation prospects for rare *C. clatratus* in Europe.

Key words: Chronogeonemy analysis, Croatia, gap analysis, habitat loss, land use change, local extinction, protected areas

Introduction

The decline of insect diversity, along with the extinction of specific taxa, is an ongoing process across Europe, driven by habitat degradation and loss, agricultural intensification, the use of insecticides, the spread of invasive species, and climate change (Habel et al. 2019; Wagner 2020). This negative trend is evident for the Golden-dimpled Ground Beetle (*Carabus clatratus*), a species now considered highly threatened and even extinct in parts of Europe (Turin et al. 2003; Casale and Busato 2008; Schmidt et al. 2016). Habitat degradation and conversion of wetlands for agricultural purposes and afforestation have caused a sharp decline in this species' populations and distribution (Desender and Turin 1989; McFerran et al. 1995). Thus, the species is endangered in Poland (Pawłowski et al. 2002), critically endangered in Croatia (Vujčić-Karlo et al. 2007) and the Czech Republic (Hejda et al. 2017) and extinct in Switzerland and Italy (Marggi 1992; Casale 2018). In Italy, the species extinction was driven by the spread of the invasive Red Swamp Crayfish (*Procambarus clarkii*), which preys on adult beetles (Casale and Busato 2008; Casale 2018). The species is protected in certain European countries, e.g. Croatia and Poland, whereas it lacks legal protection in others (Pawłowski et al. 2002; NN 80/2019).

In the genus *Carabus*, subspecies represent geographically or ecologically distinct populations, diverging due to isolation, adaptation, or drift (Homburg at al. 2013; Sota 2022). Their distribution reflects postcolonization routes, refugia or historic barriers (Sota 2022). The Golden-dimpled Ground Beetle (*C. clatratus*) is divided into several subspecies, six are recognized by Turin et al. (1993, 2003) and Březina et al. (2017), five by Kryzhanovskij et al. (1995), four by Bousquet et al. (2003), while three subspecies are acknowledged by Deuve (2021). The nominotypical subspecies was described by Carl Linnaeus, as *Carabus clatratus* in 1761 (Linnaeus 1761). Joseph Müller described one of the subspecies, *C. clatratus auraniensis*, in 1903 from the type locality Vrbica by Vransko blato in Mediterranean Croatia (Müller 1903). This subspecies is recognized by Březina (1999), Březina et al. (2017), Bousquet et al. (2003), Kryzhanovskij et al. (1995) and Turin et al. (1993, 2003), with some variation in the spelling and the year of its description. Following the International Code of Zoological Nomenclature (ICZN 1999) Principle of Priority (Article 23) and as endorsed by Turin et al. (2003) the original spelling *C. clatratus auraniensis* J. Müller, 1902 is adopted in this paper, as the inclusion of the letter 'h' is likely a nomenclatural inaccuracy that has persisted for over a century. However, some authors, such as Deuve (2021), favour the ICZN principle of maintaining incorrect subsequent spelling due to prevailing usage (ICZN 1999), using *Carabus clathratus* Linnaeus, 1761. The confusion regarding the year of the subspecies description arises because the manuscript was submitted to the "Münchner Koleopterologische Zeitschrift" in 1902, but it was not published until 1903. Thus, 1903 should be considered the valid year for the subspecies description.

In the late 19th century, *C. clatratus* was first documented for Croatian fauna by Schlosser Klekovski (1877). Several years later, Joseph Müller described *C. clatratus auraniensis* from Dalmatia (Müller 1903) and the type material is stored in the Civic Museum of Natural History, Trieste (Casale et al. 1982). A few years prior to Müller's description, Padewieth (Franjo Dobijaš, an entomologist who published several publications under the pseudonym M. Padewieth) recorded *C. clatratus*

near Rijeka (Fiume), in the Draga valley (Padewieth 1897). Recent literature has caused some confusion regarding the *locus typicus*. Deuve (2021) cites Rijeka, while Cavazzuti and Ghiretti (2020) mention both Vrana Lake and Rijeka, the latter locality not aligning with Müller's original description (Müller 1903).

Carabus clatratus auraniensis occurs in the Balkan states, Hungary and the southern parts of Austria, the Czech Republic and Slovakia, and northern Greece (Drovenik and Peks 1999; Turin et al. 2003). *Carabus clatratus* is a stenotopic and highly hygrophilous species that inhabits wetlands, open wet grasslands and pastures, and flooded lowland forests (Koch 1989; Hůrka 1996; Turin et al. 2003). It shows flight-wing dimorphism, with macropterous (fully winged) and brachypterous (short-winged) individuals present in the population (c.f. Turin et al. 2003). Moreover, it is one of the very few species within the genus that is capable of flight (c.f. Turin et al. 2003). The species exhibits a semi-aquatic lifestyle, with the first larval instar residing on land. The second and third larval instars, and particularly the adults, hunt for prey underwater (Sturani 1962; Thiele 1977; Casale and Busato 2008), implicating the importance of wetlands for the persistence of the species.

Since the mid-19th century, the European wetlands, has undergone profound changes due to increasing human pressures (Perennou et al. 2012; Čížková et al. 2013). These activities have resulted in significant habitat loss and degradation, raising concerns about their impact on threatened, highly hygrophilous taxa like *C. clatratus auraniensis*. Therefore, the objectives of this study were: 1) to assess conservation status of *Carabus clatratus auraniensis* in Western Balkans (Croatia and Slovenia) through a chronogeonemy analysis based on museum collections, literature data, and field studies; 2) to evaluate the suitability of type locality for the persistence of *C. clatratus auraniensis* by analysing land use changes in adjacent localities, using historical maps; and 3) to assess the effectiveness of national protected areas and the European Natura 2000 network in ensuring the long-term survival of *C. clatratus auraniensis* in Croatia, core area of species distribution in Western Balkans, using a comprehensive database.

Methods

Chronogeonemy, which involves the temporal and spatial examination of areal changes (Stoch 1998; Brandmayr et al. 2006), was employed to detect and reconstruct the trends of the subspecies' range in Croatia over time. This analysis is a powerful tool for identifying critical areas within a species' range, enhancing analysis reliability and providing early-warning signals that may prompt further research (Brandmayr et al. 2006). For the analysis, we compiled a comprehensive database incorporating data from field studies, scientific literature, and entomological collections. In addition, occurrence records were retrieved from the Global Biodiversity Information Facility (GBIF) database (accessed 20 Jan 2025). Records were grouped by decade and discussed within the framework of three biogeographical regions: Alpine, Continental, and Mediterranean (following EEA, 2016). Distribution data were then categorized into two groups: historic – records older than 50 years (i.e. collected before 1975), and recent – records collected within the last 50 years (i.e. from 1975 onwards).

Considering museum material, we examined the data from multiple collections, including the Croatian Natural History Museum ("Central Beetle Collection

together with Korlević Collection", "Weingartner Collection", "Coleoptera Varia Collection", "Redenšek Beetles Collection", "Perović Collection" and "Igalffy Collection") in Zagreb, Natural History Department of the Zadar National Museum ("Coleoptera Collection"), Split Natural History Museum ("Novak Collection"), Natural History Department of the Varaždin City Museum ("Koščec Collection"), Rijeka Natural History Museum ("Coleoptera Collection"), Slovenian Museum of Natural History ("Gspan Entomological Collection" and "Central collection of Slovenian beetles") in Ljubljana, and Civic Museum of Natural History ("Müller Collection", "Palearctica Collection" and "Driolli Collection") in Trieste. Additionally, we analysed data from private collections, including Toni Koren, Snježana Vujčić-Karlo and Andreja Brigić (available upon request to the owner). We transcribed museum labels, which typically included the nearest toponym, collection dates, collector information, and species identification. Records with only general geographic information (e.g. Croatia, Dalmatia, Slavonia), illegible data, or missing details were entered into the database but excluded from analyses that required complete data. When the coordinates were not available, records were georeferenced using the Register of Geographical Names of Croatia and supplemented with elevation data obtained from Free Map Tools (2024).

To ensure data integrity, duplicate records were removed, considering only distinct populations (i.e., observations from different localities and years). For historical records cited in multiple sources, only the original reference was retained (e.g., Padewieth 1897 record, later cited by Depoli (1929), Cavazzuti and Ghiretti (2020), and Deuve (2021), was counted only from its 1897 occurrence).

Land use changes at the type locality and nearby site of *C. clatratus auraniensis* (Vrbica and Biljane Donje near the Vrana Lake, Zadar, Dalmatia) were analysed using three cartographic sources: (1) the Third Military Survey of the Habsburg Empire (1869–1887) from Arcanum Maps (Biszak et al. 2007) to represent historical habitat conditions, (2) CORINE Land Cover 1980 data (Copernicus Land Monitoring Service 1980) and (3) CORINE Land Cover 2018 data (Copernicus Land Monitoring Service 2018). Polygons were drawn around wetland areas visible on the Arcanum map for each type locality. To assess land cover changes from the 1980s to the present, the area of these polygons was analysed. The CORINE Land Cover (CLC) categories were quantified within each polygon using datasets from 1980 and 2018. Categories with an area smaller than 0.1 km^2 were excluded to minimize mapping errors and dataset noise. Chi-squared test was used to determine significant changes in land use between 1980 and 2018 for the type locality and a nearby site using area percentages in R, version 4.3.3 (R Core Team 2025). Analyses were conducted at two levels of the CLC classification: broader categories (CLC Level 1) to detect general land use shifts and finer subcategories (CLC Level 3) within each Level 1 group to identify more detailed changes.

A gap analysis was conducted to assess the extent to which *C. clatratus auraniensis* records are covered by protected areas in Croatia and thus identify conservation gaps. Gap analysis is a spatial tool used to identify the coverage gaps and to evaluate the completeness of existing protected area networks (Rodrigues et al. 2004). This analysis, successfully applied to carabid beetles in previous studies (Fuller et al. 2013), was used to compare the areas of suitable habitats for the subspecies with the existing network of protected areas in Croatia (e.g. including national and nature parks and Natura 2000 sites under the

Habitats and Birds Directives) in order to identify suitable areas that remain outside formal protection. The protected area data in Croatia were imported in QGIS as a WFS layer from the Bioportal platform (Bioportal 2024), managed by the Croatian Ministry of Environmental Protection and Green Transition, while layers containing biogeographical regions (Continental, Alpine and Mediterranean) were downloaded from the European Environment Agency geospatial data catalogue (EEA 2016). The protected area layers were merged into a single layer, which was then intersected with the species records. A record was considered covered by a protected area if it overlapped with any one of them. The resulting intersected layer was compared to the records layer to calculate the percentage of records covered by protected areas, shown for each region separately. All spatial analyses and map creation were carried out using QGIS version 3.34.12.

Results

Database records

In the past 130 years, a total of 82 records of *C. clatratus auraniensis* have been collected from Western Balkans, 81 from Croatia and one from Slovenia. Among these, 18 records were associated with overly general locality names (listed simply as "Croatia", "Dalmatia", "Istria", "Slavonia" and "Continental Croatia"), which prevented the assignment of precise geographic coordinates. Additionally, two locations with broad toponyms ("Mirna" and "Vransko blato") were georeferenced, but due to insufficiently detailed locality descriptions, these coordinates may not be completely accurate. In total, 28 records were identified as historical (prior to 1975), 17 of which could not be georeferenced. Among the 45 recent records, only one has no sufficient data for coordinate assignment. Ten records were found through a literature review, 56 from entomological collections (26 from museum collections and 33 from private collections), and four records were based on direct field observations. No record of this species was found in the GBIF database (GBIF 2025).

Assessment of historical distribution in Croatia and Slovenia

Carabus clatratus auraniensis has been documented in two biogeographical regions of Croatia: the Mediterranean and Continental regions (Fig. 1A, B), mainly in wetland habitats (Fig. 1C, D), while in Slovenia it has been found exclusively in the Continental biogeographical region (Table 1). No records have been observed for the Alpine biogeographical region so far in either country.

Within the Mediterranean region, the species has only been recorded on mainland, with no records found in Adriatic islands. In the region, only six records have been documented: three records in northern Dalmatia near Zadar and two records in the Istrian Peninsula and one record in the northern Adriatic region near Rijeka (Fig. 1B, Table 1). The locality Vrbica (Vransko blato) represents the subspecies' type locality (Müller 1903), while Biljane Donje locality is found near the Vrana Lake. Moreover, the species was collected in these localities by Petar Novak in 1903 and 1904 (Table 1).

In the Continental region, *C. clatratus auraniensis* has been recorded at 16 localities (Fig. 1B). The earliest known record with precise location details dates

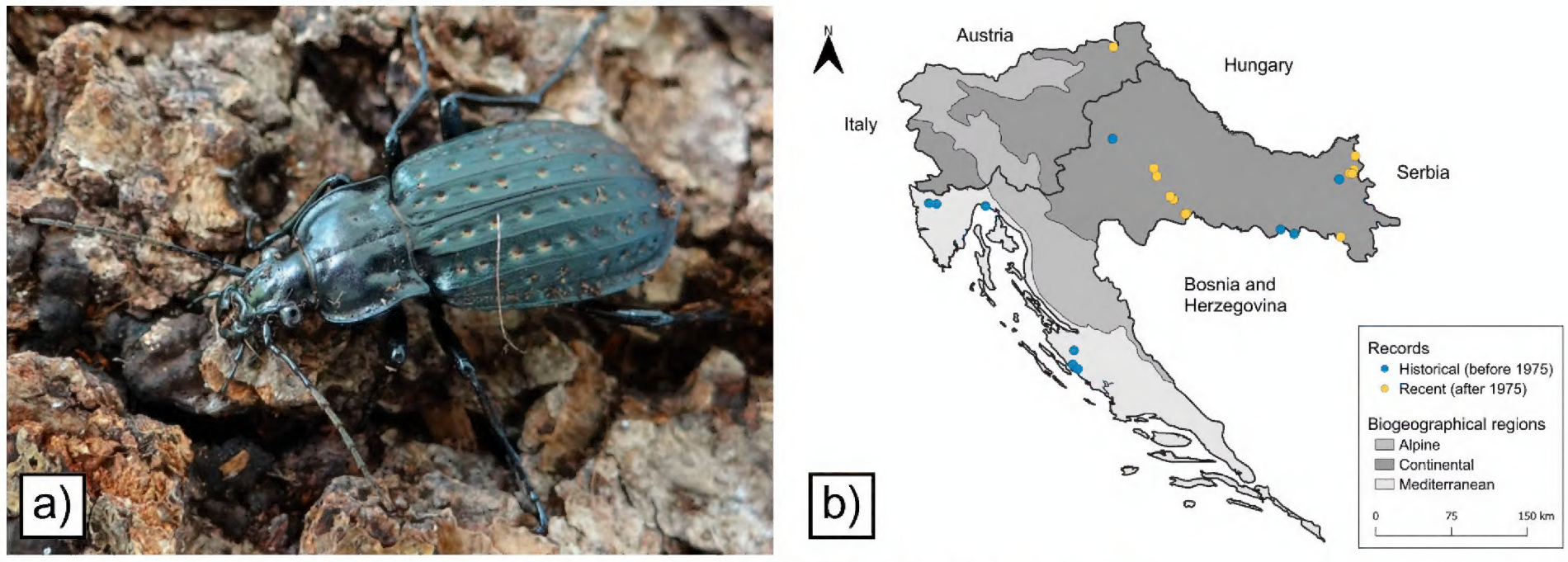

Figure 1. Habitus, spatial distribution and habitats of *Carabus clatratus auraniensis* J. Müller, 1903. **A.** *Carabus clatratus auraniensis* J. Müller, 1903 found in the flooded lowland forest Žutica, Pepelana (photo: T. Koren); **B.** Spatial distribution of *C. clatratus auraniensis* J. Müller, 1903 across Croatia and Slovenia, with historic records (before 1975) shown by blue dots and recent records (after 1975) by yellow dots, with varying shades of grey indicating biogeographical regions; habitats of *C. clatratus auraniensis* J. Müller, 1903 in Croatia; **C.** Forest remnant and pasture, Lonjsko polje Nature Park (photo: A. Brigić, November 2004); **D.** Flooded lowland forest Žutica, Pepelana (photo: T. Koren, March 2017).

back to March 1896 in Osijek (Langhoffer 1899). Another specimen, collected in May 1896 in Osijek, is preserved in the "Central Beetle Collection together with the Korlević Collection" in the Croatian Natural History Museum, with no details about the collector (Table 1). Most records in this region were documented along the middle and lower reaches of the Sava River, namely from the Lonjsko polje Nature Park (Fig. 1C), or with the lower reach of the Drava River and the middle reach of the Danube River, most of them from the Kopački rit Nature Park (Fig. 1D). An interesting historical record is associated with the city of Zagreb, specifically the Sljeme area (the Medvednica Nature Park), with the specimen preserved in the Croatian Natural History Museum (Table 1).

A record from Slovenia obtained in 2007 was the only known record from the Mura River in Continental biogeographical region far from known populations in Croatia (Table 1). The specimen, stored in the collection of Slovenian Museum of Natural History, was winged.

Carabus clatratus auraniensis was mainly found at low altitudes, up to 200 m in both the Continental and Mediterranean regions of Croatia. An exception is the record from Zagreb, on Medvednica Mountain (Sljeme, 1029 m a.s.l.), collected in 1900.

Table 1. Records list of *Carabus clatratus auraniensis* J. Müller, 1903 in Western Balkans (Croatia and Slovenia). Broad toponyms are shown in italic and locus typicus in bold. Legend: AB Collection: Andreja Brigić Collection; SVK Collection: Snježana Vujčić-Karlo Collection; TK Collection: Toni Koren Collection; CNHM: Croatian Natural History Museum (Zagreb); NMZ: National Museum Zadar; CMNH: Civic Museum of Natural History, Trieste; PMS: Slovenian Museum of Natural History, Ljubljana; – no data.

Biogeographical region	Locality	Date	Year	Data source
Continental	Slavonia	1877	1877	Schlosser Klekovski (1877)
	Continental Croatia	1877	1877	Schlosser Klekovski (1877)
	Osijek	–	–	Weingärter Collection (CNHM)
		22.03.1896	1896	Langhoffer (1899)
		22.05.1896	1896	Central Beetle Collection together with Korlević Collection (CNHM)
	Sljeme, Zagreb	05.05.1900	1900	Central Beetle Collection together with Korlević Collection (CNHM)
	Klakar, Slavonski Brod	08.1910	1910	Central Beetle Collection together with Korlević Collection (CNHM)
	Slavonski Brod	–	–	PMS: Gspan Collection
	Krapje Đol (Lonjsko polje)	15.05.1985	1985	Coleoptera Collection (NMZ)
	Drenov Bok (Lonjsko polje)	18.03.1999	1999	SVK collection
	Drenov bok, near Krapje Đol Ornithological reserve (Lonjsko polje)	19.05.2000	2000	AB collection; Brigić et al. (2014)
		16.09.2000	2000	AB collection; Brigić et al. (2014)
	Hordovanj (Kopački rit)	24.08.2001	2001	SVK collection
		31.07.2003	2003	Domić (2009)
	Jezero Sakadaš (Kopački rit)	05.05.2001	2001	SVK collection
		24.08.2001	2001	SVK collection
	Mužilovčica (Lonjsko polje)	10.05.2002	2002	AB collection; Brigić et al. (2024)
		24.05.2002	2002	AB collection; Brigić et al. (2024)
		21.06.2002	2002	Coleoptera Collection (NMZ); SVK collection; Brigić et al. (2024)
		10.07.2002	2002	Coleoptera Collection (NMZ); AB collection; SVK collection; Brigić et al. (2024)
		24.07.2002	2002	SVK collection; Brigić et al. (2024)
		18.08.2002	2002	AB collection; Brigić et al. (2024)
		04.09.2002	2002	AB collection; Brigić et al. (2024)
		18.09.2002	2002	SVK collection; Brigić et al. (2024)
		17.10.2002	2002	AB collection; Brigić et al. (2024)
	East Slavonia			Turin et al. (2003)
	Zmajevac (Slavonia)	29.07.–15.08.2003	2003	Talóssi (2008)
	Gornja Radgona, Police (NE Slovenia)	20.6.2007	2007	PMS: Central collection of Slovenian beetles; Vrezec et al. (2007)
	Žutica forest, Crna Jaruga	29.09.2017	2017	TK collection
	Žutica forest, Okoli village, toponim Pepelana	27.09.2017	2017	TK collection
	Čigoč, Lika (Lonjsko polje)	2018	2018	Zadravec (2018)
	Batina (Kopački rit)	04.06.2021	2021	TK collection
	Županja	2021	2021	Retezár and Szél (2021)
Mediterranean	Dalmatia	1877	1877	Schlosser Klekovski (1877)
	Draga Valley (near Rijeka, Primorje)	1897	1897	Padewieth (1897); Depoli (1929); Cavazzuti & Ghiretti (2020); Deuve (2021)
	Vrbica (Vranjsko blato)	04.1902	1902	Müller Collection (CMNH); Müller (1903); Novak (1952); Casale et al. (1982)
	Vranjsko blato	–	–	Müller Collection (CMNH)
	Biljane Donje (near Vrana Lake, Dalmatia)	14.07.1904	1904	Novak (1952)
	Istria	1932	1932	Winkler (1932)
	Mirna Valley (Istria)	20.05.1923	1923	Palearctica Collection (CMNH); Müller (1926); Cavazzuti and Ghiretti (2020)
	Livade (Istria)	03.03.1968	1968	Driolli Collection (CMNH)
		03.07.1968	1968	Driolli Collection (CMNH)
	North Dalmatia			Turin et al. (2003)

Chronogeonemy analysis

The chronogeonemy analysis (Fig. 2) has yielded several important findings: a) no *C. clatratus auraniensis* records exist in the Mediterranean biogeographical region since 1968, and no records from the type locality for 120 years; b) a significant decline in records occurred between the two World Wars and the post-war period; c) a sharp increase in records was observed from 2000 in the Continental biogeographical region; and d) the number of *C. clatratus auraniensis* populations is rather low throughout the timeline (Fig. 2).

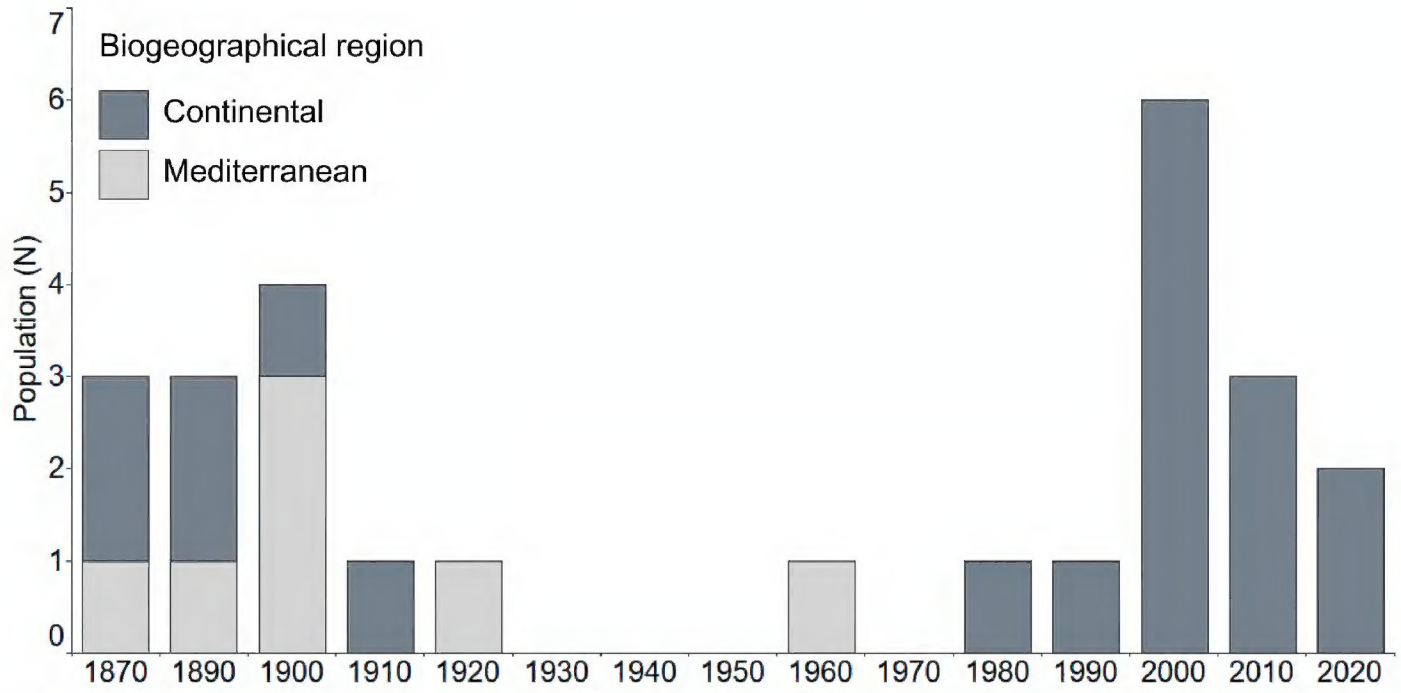

Figure 2. Chronological analysis with the biogeographical distribution of *Carabus clatratus auraniensis* J. Müller, 1903 in Croatia. Population size was estimated by counting the number of unique populations per decade and per region.

Land use changes at the sites close to the type locality

A comparison of historical maps dating from around the time of the subspecies' description, with recent geographical maps of the Vrana Lake area reveals a significant habitat alteration (Fig. 3; Table 2). It is evident that extensive wetland drainage for agricultural purposes has occurred over time (Figs 3, 4; Table 2). The once-wide wetland areas surrounding the Vrana Lake (Fig. 3A, D) have been largely converted into agricultural land (Fig. 3B, E), and the remaining wetlands are now restricted to a narrow strip along the lake's northwestern edge, as shown by CORINE Land Cover analysis (Fig. 3C; Table 2). A closer examination of the Vrana Lake area in the late 19th century, where Joseph Müller and Petar Novak recorded the species near Vrbica in 1903 (type locality), reveals the existence of a wetland, Vransko blato, which had been fully drained (Fig. 3A–C; Table 2). A similar trend is observed at Biljane Donje, where *C. clatratus auraniensis* was collected in 1904, the area that formerly supported extensive wetlands Terljuge, which had also been drained (Fig. 3E–G; Table 2).

Between 1980 and 2018, the landscape continued to change near the Vrana Lake (Vrbica and Biljane Donje settlements). In Vrbica, no significant differences were found between the broader CLC Level 1 categories ($x^2 = 4.31 \times 10^{-5}$, $p > 0.05$). However, significant changes were detected within the agricultural area category ($x^2 = 107.62$, $p < 0.001$), particularly with a complete shift from complex cultivation patterns to non-irrigated arable land, while wetlands remained

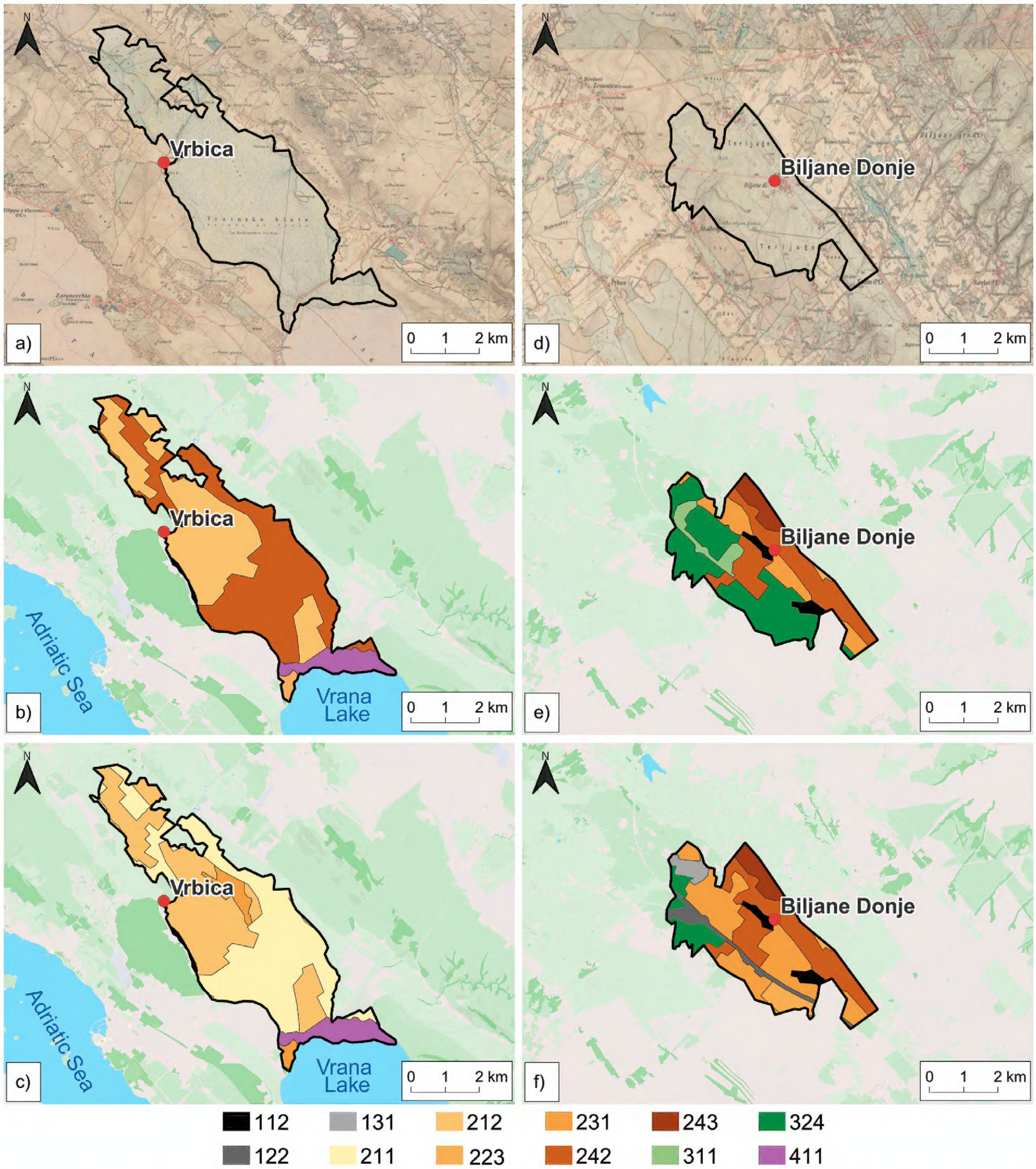

Figure 3. Historic and recent land cover at first known *C. clatratus auriensis* sites in Croatia. Distribution of *Carabus clatratus auraniensis* J. Müller, 1903 in Croatia, with records from the Vrbica and Biljane Donje localities, the first known records of the species in the country. **A–C.** Vrbica: historical map (1869–1887), CORINE Land Cover (1980), and CLC (2018); **D–F.** Biljane Donje in the same format. Light green areas on the historical maps indicate wetland habitats. Legend: 112 – Discontinuous urban fabric, 122 Road and rail networks and associated land, 131 – Mineral extraction sites, 211 – Non-irrigated arable land, 212 – Permanently irrigated land, 223 Olive groves, 231 – Pastures, 242 – Complex cultivation patterns, 243 – Land principally occupied by agriculture, with significant areas of natural vegetation, 311 – Broad-leaved forest, 324 – Transitional woodland/shrub, 411 – Inland marshes.

largely unchanged (Table 2; Fig. 4A). In contrast, Biljane Donje exhibited significant changes at both CLC Level 1 ($x^2 = 41.45$, $p < 0.001$), showing a decline in forest and semi-natural areas and an increase in agricultural areas. Changes within all categories ($p < 0.001$) suggest an ongoing land cover transforma-

Table 2. Spatio-temporal changes in land use categories at first known *Carabus clatratus auriensis* J. Müller, 1903 sites in Croatia. Changes in the area of different CORINE Land Cover categories between 1980 and 2018 tested with Chi-Square test. Significant values are indicated in bold.

Locality	CORINE Land Cover categories		Area in km²			χ² test between CLC 1 categories		χ² test between CLC 3 categories	
	CLC level 1	CLC level 3	1980	2018	Change	χ²	p-value	χ²	p-value
Vrbica	Artificial surfaces	Discontinuous urban fabric (112)	0.114	0.114	0.000	4.31×10^{-5}	1.00	N/A	N/A
	Agricultural areas	Non-irrigated arable land (211)	0.000	11.678	-11.678			**107.62**	**< 0.001**
		Permanently irrigated land (212)	10.113	9.468	+0.645				
		Pastures (231)	0.319	1.104	-0.785				
		Complex cultivation patterns (242)	11.808	0	+11.808				
	Wetlands	Inland marshes (411)	1.632	1.628	+0.004			N/A	N/A
Biljane Donje	Artificial surfaces	Discontinuous urban fabric (112)	0.559	0.558	+0.001	**41.45**	**<0.001**	**116.90**	**< 0.001**
		Road and rail networks and associated land (122)	0.000	0.997	-0.997				
		Mineral extraction sites (131)	0.000	0.573	-0.573				
	Agricultural areas	Olive groves (223)	0.000	0.743	-0.743			**17.39**	**< 0.001**
		Pastures (231)	1.942	5.499	-3.557				
		Complex cultivation patterns (242)	4.309	4.564	-0.255				
		Land principally occupied by agriculture with significant areas of natural vegetation (243)	0.894	0.894	0.000				
	Forests and semi-natural areas	Broad-leaved forest (311)	0.920	0.000	+0.920			**11.16**	**< 0.001**
		Transitional woodland/shrub (324)	6.506	1.301	+5.205				

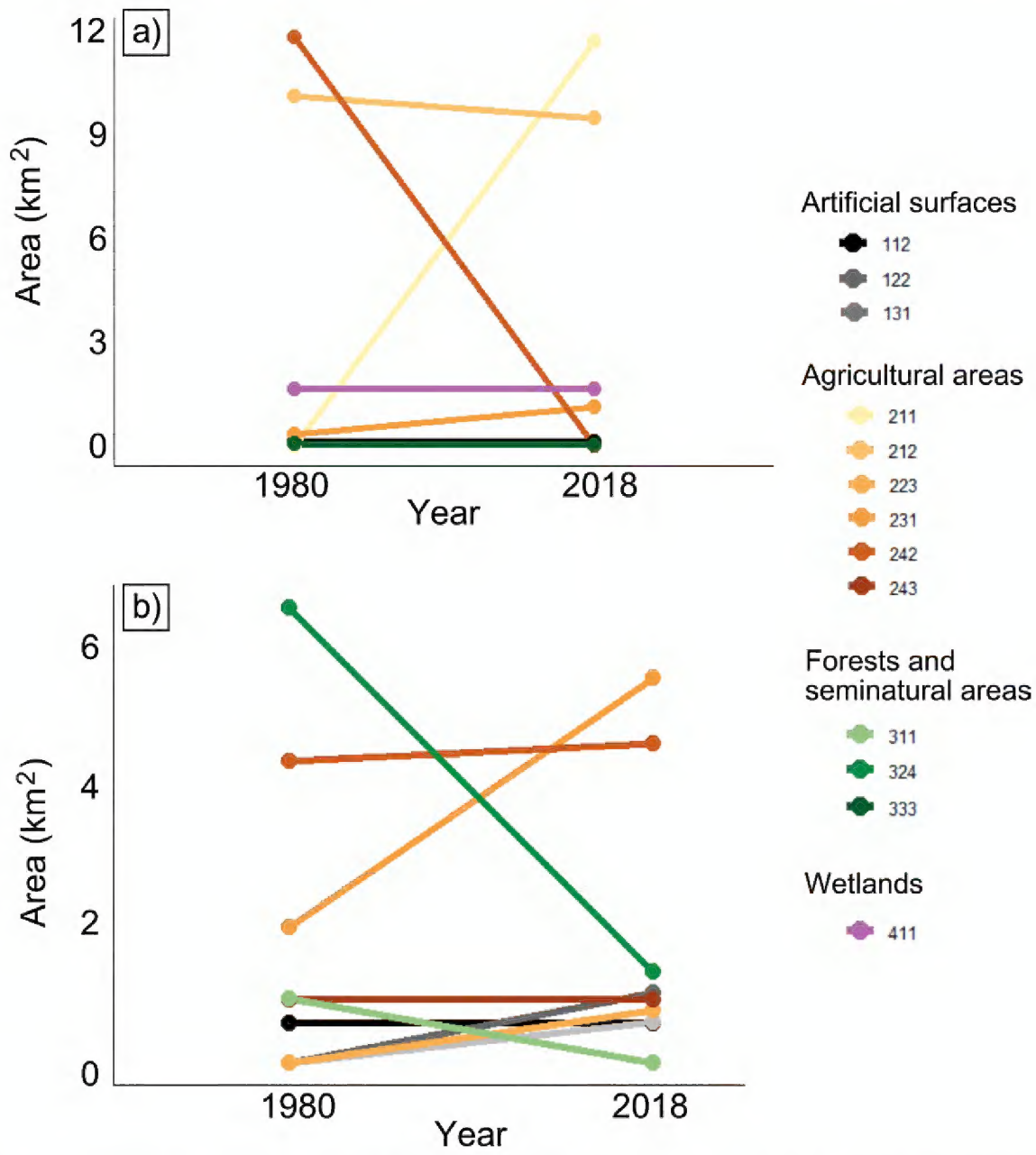

Figure 4. Temporal changes in land cover categories at first known *C. clatratus auriensis* sites in Croatia. Changes in the area of different CORINE Land Cover categories between 1980 and 2018. **A.** Vrbica, the type locality; **B.** Biljane Donje, nearby site. Legend: 112 – Discontinuous urban fabric, 122 Road and rail networks and associated land, 131 – Mineral extraction sites, 211 – Non-irrigated arable land, 212 – Permanently irrigated land, 223 Olive groves, 231 – Pastures, 242 – Complex cultivation patterns, 243 – Land principally occupied by agriculture, with significant areas of natural vegetation, 311 – Broad-leaved forest, 324 – Transitional woodland/shrub, 333 – Sparsely vegetated areas, 411 – Inland marshes.

tion in Biljane Donje towards altered/managed habitats, visible especially in the elimination of broad-leaved forests, decrease of transitional woodland/shrub and an increase in pastures (Table 2; Fig. 4B).

Gap analysis

Gap analysis indicate a good efficiency of Croatia's protected areas in covering the distribution of *C. clatratus auraniensis* (Fig. 5, Table 3). Protected areas covered most of the species' known occurrences across both the Continental and Mediterranean biogeographical regions, with more records found within protected areas in the Continental region than in the Mediterranean (Table 3).

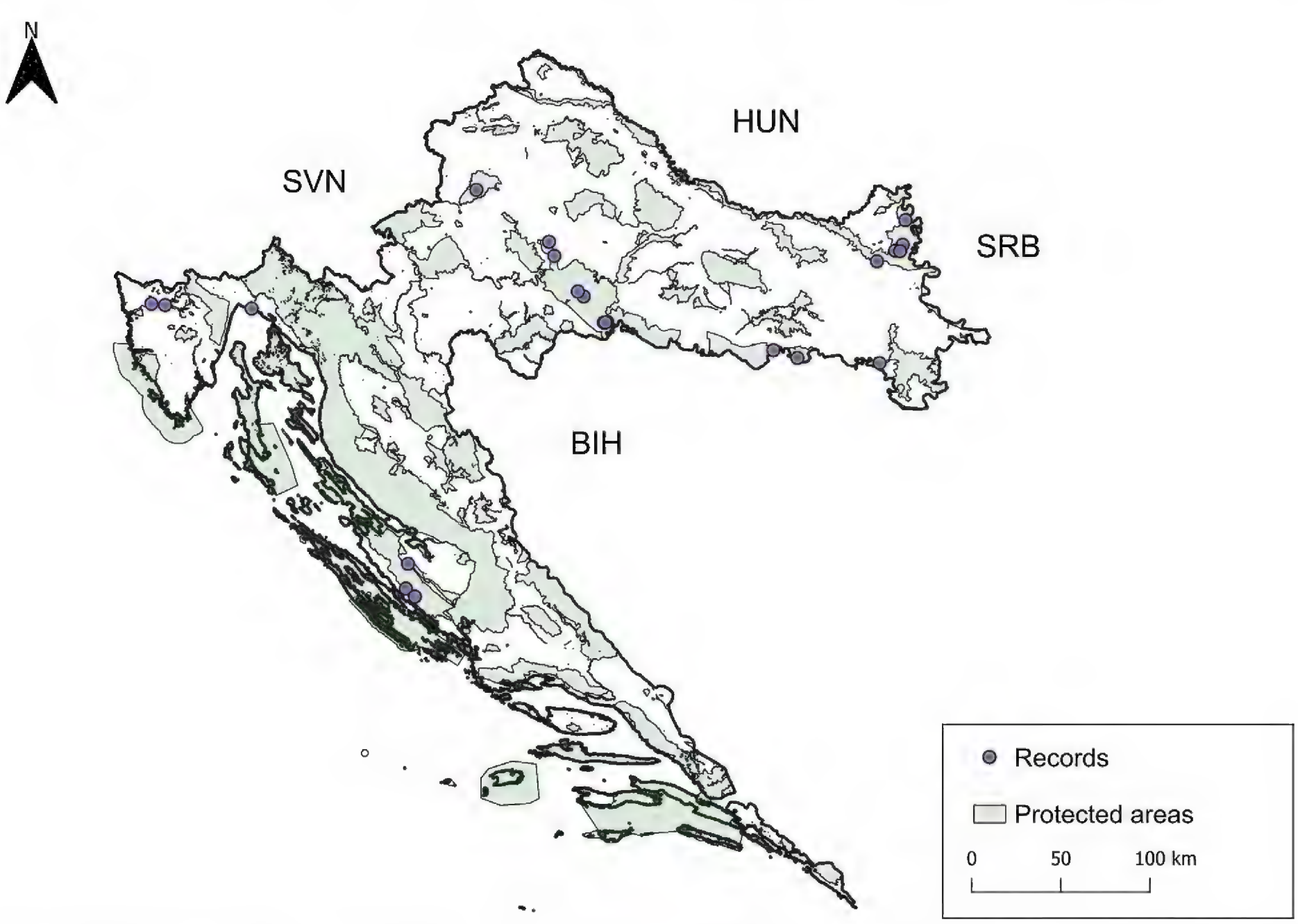

Figure 5. Gap analysis of *C. clatratus auriensis* in Croatia. Distribution of *Carabus clatratus auraniensis* J. Müller, 1903 records in Croatia (purple dots) overlapped with the following protected areas: Croatian national and nature parks, Natura 2000 sites under the Habitats and Birds Directives (green surfaces).

Table 3. Number of records of *Carabus clatratus auraniensis* J. Müller, 1903 within protected areas (national and nature parks, Natura 2000 sites under the Habitats and Birds Directives) across Croatian biogeographical regions, divided by the total number of records for each biogeographical region and combined across all regions.

Biogeographical region	Locations in protected areas	Locations outside protected areas	Total
Alpine	0	0	0
Continental	14 (88%)	2 (12%)	16
Mediterranean	4 (67%)	2 (33%)	6
All regions	18 (82%)	4 (18%)	22

Discussion

The present study reveals: 1) chronogeonemy analysis indicated the extinction of *C. clatratus auraniensis* in the Mediterranean biogeographical region of Croatia; 2) large wetland habitats in the Continental biogeographical region support the continued persistence of *C. clatratus auraniensis*; 3) the outcomes of the chronogeonemy analysis contradict the results of the gap analysis, suggesting that current conservation measures may underestimate or overlook localised extinctions and habitat suitability.

Conservation status of *Carabus clatratus auraniensis* in Croatia

Our results indicate *C. clatratus auraniensis* extinction in the Mediterranean biogeographical region of Croatia, as it has not been recorded in the region for 68 years and at the type locality for more than 120 years. This absence persists despite extensive surveys of carabid beetle assemblages in wetland or riparian habitats throughout the region (Durbešić 1983, 1990; Durbešić et al. 1995, 1998) including areas around the Vrana Lake (Vujčić-Karlo 2006, 2008, 2010, 2012) and the Istrian Peninsula (Brigić et al. 2023c; Šerić Jelaska et al. 2023). Moreover, the type locality – the Vrana Lake was sampled using various sampling methods (more than 85 pitfall traps and hand sampling) during the vegetation season, but the species was not recorded (Vujčić-Karlo 2008). The apparent local extinction is most likely related to the extensive habitat change in the Mediterranean biogeographical region. The Mirna Valley in Istria has been significantly altered in the last two centuries by human interventions such as dredging of the riverbed, construction of the Butoniga reservoir and deforestation to expand agriculture (Bragato et al. 2004). These measures changed the hydrological system of the valley, negatively impacting the forest lowland ecosystem in the Mirna Valley (Bragato et al. 2004; Koren et al. 2015). In Dalmatia, the drainage of wetlands and the expansion of agriculture around the type locality, Vrana Lake, were clearly documented in this study by comparing historical and current maps. One of the best-known examples is Terljuge, a large Mediterranean wetland, whose conversion to farmland began in 1770 with the construction of the Prosika Canal. This intervention enabled the water drainage from Vrana Lake into the Adriatic Sea by lowering the water level of the lake by approximately three meters. At the beginning of the 19th century, further changes were made by deepening the Canal. The comprehensive land reclamation project, completed in 1948, included the widening and further deepening of the Prosika Canal and the construction of an extensive drainage network throughout the area. As a result, the wetland ecosystem was almost completely converted to agricultural land, with the exception of a narrow zone adjacent to the remaining lake area (Mesić 2006). The loss of suitable wetland habitats documented for *C. clatratus auraniensis* is consistent with trends in Europe, where wetland degradation has led to significant declines and local extinctions of several insect taxa, especially in Dytiscidae (Ribera et al. 1996), Odonata (Grand 1996) and Lepidoptera (Sommer et al. 2022).

While the trend in conservation status in the Mediterranean biogeographical region is unfavourable, it remains stable in the Continental region. This

is suggested by the continuous occurrence of the species in the Continental region of Croatia since the late 19th century, with the exception of the period between the two World Wars and after the Second World War, when entomological research declined and/or interest in the study of terrestrial invertebrates was limited (Durbešić 2011). Consequently, few studies have been conducted for some regions and decades, which may influence the presence/absence of the species. However, there was a remarkable increase in records in the last three decades, especially between 2000 and 2010, reflecting the good prospects of *C. clatratus auraniensis* in terms of area and population size. Despite more intensive research this increase may be partly even a consequence of population increase stimulating species dispersal even to more distant areas, e.g. record by Mura River in Slovenia in 2007. As this specimen was winged with no other specimen found in the area despite intensive sampling within the monitoring programme of *Carabus variolosus* wetland habitats between 2007–2024 (Vrezec et al. 2024), we regard this record as accidental with no established population in Slovenia. Most records of *C. clatratus auraniensis* have been documented along the Sava, Danube and Drava Rivers, in the Lonjsko polje and Kopački rit Nature Parks, both of which are Ramsar-listed wetlands (Ramsar 2024). These nature parks represent two of the largest remaining wetland complexes and best-preserved semi-natural habitats in the Danube Basin, serving as important refuges for rare and endangered species and supporting rich biodiversity within their extensive ecosystems (Mrakovčić et al. 2006; Tutiš et al. 2013; Brigić et al. 2014, 2024; Turić et al. 2021). In this region, the species inhabits open wet grasslands and pastures, reedbeds and flooded lowland forests (Tallósi 2008; Brigić et al. 2014, 2024). It also occurs in shrubby vegetation near various water bodies dominated by *Salix* spp., *Fraxinus angustifolia* and *Quercus robur* (Brigić et al. 2014; Zadravec 2018). The occurrence of *C. clatratus auraniensis* in the Lonjsko polje NP is favoured by traditional land management practices, such as livestock grazing and pigs rooting (Brigić et al. 2024). Livestock create micro-depressions that fill with water, maintaining a mosaic of wetland microhabitats that is crucial for the survival of the species (Brigić et al. 2024).

The subspecies has not been recorded in the Alpine region of either country, which is in line with Pavičević and Mesaroš (1997). Although it occasionally occurs at elevations of up to 2000 metres a.s.l., such as Anatolia and the Caucasus, it is primarily a lowland species (Turin et al. 2003). Moreover, the subspecies *C. clatratus auraniensis* has not been recorded in Croatian peatlands despite extensive surveys of these habitats in all biogeographical regions (Brigić et al. 2017, 2023a, b). However, the nominotypical subspecies is classified as tyrphophilous or peat inhabiting species in W Europe (Peus 1928; Turin et al. 2003). It has been proposed as a potential indicator species for the quality of peat bogs and wetlands (Anderson et al. 2000; Woodcock et al. 2004).

Among the records we examined, the species was predominantly found at lower altitudes, supporting previous findings (Jeannel 1941; Casale et al. 1982). An exception is a historical record labelled “Sljeme”; however, in the context of the collection, this toponym often refers to the entire Medvednica Mountain rather than the summit, as specimens were typically collected along the ascent. Therefore, the exact elevation of this record remains uncertain. Recent studies of carabid beetles along the Medvednica streams have not

documented the presence of *C. clatratus auraniensis* (Brigić et al. 2023b; Šerić Jelaska et al. 2023). Over the past century, habitats in proximity to Zagreb have been significantly altered by urbanisation, agriculture, watercourse regulation, and other anthropogenic factors. As a result of habitat homogenisation, several species typical of wetland habitats have become critically endangered or regionally extinct, as documented for insect, e.g. *Nymphalis xanthomelas* and plant species, e.g. *Calla palustris*, *Galium uliginosum*, *Drosera intermedia* etc. (Mihelj et al. 2005; Šegulja and Palković 2005; Topić and Štefan 2005; Štih et al. 2011; Šašić et al. 2015).

Contradictions between gap and chronogeonemy analysis

This study shows that chronogeonemy analysis may reveal local extinctions and habitat changes overlooked by gap analysis and current conservation tools. In the Mediterranean biogeographical region, localities where *C. clatratus auraniensis* had been recorded became protected from 1983 onwards, including the establishment of the Ornithological Reserve in Vrana Lake (1983), Vrana Lake Nature Park (1999), and Natura 2000 sites (SO Biograd na moru 1983; NN 77/99; NN 80/2019). However, these conservation measures were implemented too late for this highly stenotopic, hygrophilous beetle, which became extinct in the region due to changes in land use that took place before the establishment of protected areas. Thus, to develop a plan of reestablishment of the population of *C. clatratus auraniensis* at restored sites in the Mediterranean region by reintroductions of specimens from Continental Croatia is highly recommended.

The gap analysis reveals effectiveness in protecting this species within the current network of protected areas in the Continental biogeographical region of Croatia. Due to high specialisation and specific ecology of *C. clatratus auraniensis*, the species stands out as a potential flagship and umbrella species for wetland nature parks in the Continental region. The habitats of *C. clatratus auraniensis* are highly threatened, yet they are also of exceptional value due to the presence of other endangered species e.g. crustaceans living fossils *Triops cancriformis* and *Lepidurus apus* (order Notostraca), and endangered beetles (Kojaković and Gottstein Matočec 2003; Turić et al. 2021), further underscoring their importance for the conservation of biodiversity in the area.

Conclusions

As a highly stenotopic species with narrow habitat requirements the Golden-dimpled Ground Beetle faces a high risk of extinction, primarily driven by the loss and degradation of its wetland habitats (Turin et al. 2003). However, despite its alarming conservation status in Europe (Marggi 1992; Pawłowski et al. 2002; Vujčić-Karlo et al. 2007; Hejda et al. 2017; Casale 2018), the species remains unprotected by any specific regulations at the EU level. Considering the observed extinction trends across Europe, there is a great need to revise species conservation status at IUCN Red-list, where the conservation assessment of carabid beetles is still lacking. In areas free from invasive crayfish, the protection of wetlands, especially through the exclusion of draining, is of fundamental importance for the protection of *C. clatratus auraniensis*. As the invasive Red Swamp Crayfish (*P. clarkii*) has not been recorded in Mediterranean

wetlands of Croatia (Maguire et al. 2018), and given that *C. clatratus* has high reproductive potential and was successfully reintroduced in Italy (before local crayfish invasion; Busato 2022), rearing and reintroduction of the species in suitable habitats of the Mediterranean biogeographic region (e.g. Vrana Lake) could enhance the species' future chance of survival.

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The authors have declared that no competing interests exist.

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Use of AI

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Data availability

Data are available from the corresponding author upon reasonable request.

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